Chapter 4

Dispersal of fungal spores through the air

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INTRODUCTION

Fungal spore dispersal can rarely be considered alone and is usually a combination of at least some of the key stages in the aerobiology pathway (Edmonds and Benninghoff, 1973), i.e., source, take-off, dispersal, deposition and effect. In this chapter we will consider the three steps needed to transport a spore, through the air, from one place another, namely: how the spore gets into the air, how it is transported through the air and how it is deposited at its final destination. Many examples of spore dispersal studies, used here, have been made in outdoor environments but the same principles apply to indoor applications to identify sources of microbial contamination in food processing situations.

Air flow considerations

Like all fluids, the flow of air can be in one or two modes: "laminar" where the air molecules follow parallel paths; and "turbulent" where the flow is more chaotic and the molecules follow different paths, although in the same general direction. Laminar flow is usually associated with low velocities and smooth surfaces, and rarely occurs outside wind tunnels or other specialised facilities (Grace, 1977). Therefore in most environments, especially outdoors, air flow is turbulent, and it is the effects of turbulence that are largely responsible for the dispersal of spores carried in the air. However, when air flows over a surface, friction slows it down so that the airspeed decreases as the surface is approached (Figure 1). The area of transition from free air flow to the surface is known as the boundary layer. Very close to the surface the air flow becomes laminar (laminar sub-layer) and air speed is almost zero (Grace, 1977). The thickness of this "boundary layer" depends on the nature of the flow over the surface and the structure of the surface itself. Air flow over surfaces has been extensively studied, and flow over natural surfaces such as leaves is discussed by Monteith and Unsworth (1990). The existence of the surface boundary layer has consequences for spore release and dispersal and is discussed below.

On a different scale, in the atmosphere, wind speed increases with distance above the surface as frictional forces have a decreasing effect on atmospheric flow. This layer is called the "planetary boundary layer" and extends from the surface to where friction-induced turbulence is effectively zero (Figure 1).

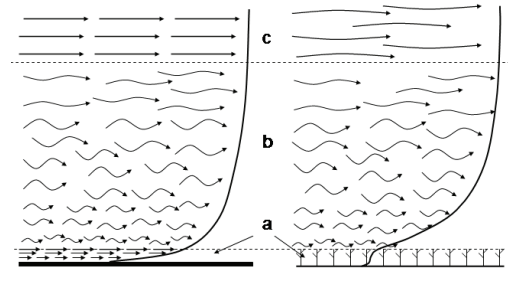

Figure 1. Left: Laminar air flow over a flat plate: (a) laminar sub-layer close to the surface; (b) turbulent boundary layer; (c) laminar free air flow. Right: Atmospheric flow over a crop: (a) surface layer within crop; (b) planetary boundary layer (turbulent); (c) pressure gradient air flow. The lines represent the wind speed profiles above the plate and the crop. Adapted from Grace (1977) and McCartney and Fitt (1985).

Sometimes the boundary layer is defined by a well-marked temperature inversion, at other times no clearly marked delineation exists and turbulence decreases gradually with increasing height. However, in the presence of large scale convection there may be significant vertical transport and the boundary layer can "break down" (Pasquill and Smith, 1983). Synoptic weather fronts and flow over mountain ranges can also cause boundary layer breakdown. The depth of the boundary layer changes in response to changes at the surface and is typically between 400 and 2000 m during the day and from a few tens of metres to about 400 m at night. Air flow within the planetary boundary layer can be very complex and is influenced not only by the physical nature of the underlying surface but also by thermal effects such as large scale convection. The nature of air flow in the planetary boundary layer had been extensively studied and the reader is referred to standard texts on atmospheric dispersal such as the publication by Pasquill and Smith (1983).

The dispersive ability of wind depends on its turbulence structure: the larger the vertical component of turbulent eddies, the greater the potential for spores to be transported into the atmosphere. Eddy structure is influenced by the thermal stability of the layer. Under neutral stability a rising air parcel remains in thermal equilibrium with the surrounding air and turbulence is dominated by friction, here the magnitude of the vertical and horizontal fluctuations in wind speed are similar (Figure 2) (Monteith and Unsworth, 1990). In contrast, in unstable conditions a rising air parcel tends to continue to rise and vertical motion is enhanced (Figure 2). Unstable conditions occur when the surface is heated, usually during the day. Conversely, under stable stratification, for example during a clear night with light winds, a rising air parcel becomes cooler than the surrounding air due to expansion as pressure decreases and so it tries to descend, thus repressing vertical motion. In this case, the vertical fluctuations in wind speed are smaller than the horizontal fluctuations (Figure 2). During the day, the air near the ground is often unstable, thus spores released during the day are more likely to be more efficiently dispersed than spores released at night. Once spores are transported above the planetary boundary layer, they have the potential to be dispersed over very large distances in large scale atmospheric motion.

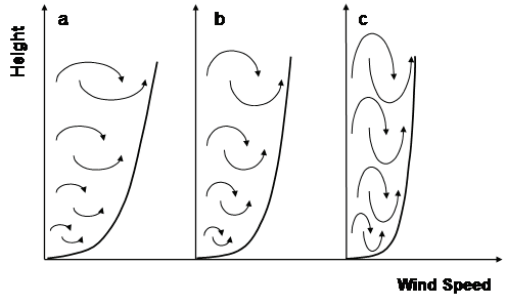

Figure 2. The influence of atmospheric thermal stability on wind speed and turbulence. (a) Stable conditions: vertical air motion is suppressed; (b) neutral stability: vertical and horizontal fluctuations are of a similar magnitude; (c) unstable conditions: vertical mixing is enhanced. Adapted from Thom (1975).

AERODYNAMIC CHARACTERISTICS OF FUNGAL SPORES

As fungal spores are much denser than air, they will naturally fall through the air under the force of gravity. The rate at which they fall plays an important role in the dispersal and deposition of airborne spores. Spores that fall quickly will tend to be less efficiently dispersed and more readily deposited than those that fall slowly. Any object falling through the air will eventually reach a steady speed, v_s, called the "settling speed", "fall speed", or "terminal velocity", when the forces of gravity are balanced by drag and lift forces that tend to slow the object down. The settling speed of a spore depends on its physical properties: mass, size and shape. However, environmental factors such as temperature or humidity can have small effects by altering the density of air or the spore itself. The gravitational forces acting on a spore are determined by its mass, while the drag forces depend on the size and shape of the spore. For objects such as winged seeds, lift forces can become important as the seed rotates or glides, but fungal spores are usually small enough for

viscous drag to be dominant. Fungal spores occur in a wide range of shapes and sizes (see plates 6 and 7, Gregory, 1973). Many fungal spores have compact shapes and can be approximated to spheres (e.g., *Aspergillus* spp., diameter 2-3 μm; *Penicillium* sp., diameter ≈ 5 μm; *Puccinia striiformis,* diameter 20-25 μm) or ellipsoids (e.g., *Sclerotinia sclerotiorum* ascospores, 8 μm long, x 3 μm diameter; *Blumeria graminis* conidia, 30 μm long x 10 μm diameter). Other spore types are more elongated and behave more like cylinders (e.g., *Helminthosporium* sp., 80 μm long x 15 μm diameter) or fibres (*Claviceps purpurea*, ≈1 μm diameter, 80-120 μm long). Some have more complex shapes, for example the conidia of some *Alternaria* sp. are club shaped. The settling speeds of fungal spores range from less than 0.1 cm s^{-1} (*Aspergillus fumigatus* spores ~ 0.03 cm s^{-1}) to over 2 cm s^{-1} (*Helminthosporium sativum* conidia 2.0-2.78 cm s^{-1}) (Gregory, 1973). For a given species the settling speed of the spores can generally be estimated only within ± 20% due to natural variation in spore sizes and moisture content, which can be affected by the ambient relative humidity.

Although v_s for many fungal spores has been measured experimentally (Gregory, 1973), it can often be estimated from physical principles if the shape and density of the spore are known (Chamberlain, 1975; McCartney, 1990; McCartney, 1997). In this approach the gravitational forces acting on the particle are equated to the drag (and if appropriate the lift) forces acting on the spore. For spherical spores of diameter d, v_s, can be calculated from Stokes' law (Chamberlain, 1975):

$$v_s = \frac{d^2 g \rho}{18 \nu \rho_a} \qquad (1)$$

where g is the acceleration due to gravity (9.81 m s^{-2}), ρ and ρ_a are the densities of the spore and air, respectively, and ν is the kinematic viscosity of air. The density of spores depends on the species and can vary with relative humidity, but many spores have densities close to that of water (Gregory, 1973). The settling speed (cm s^{-1}) of a spherical spore that has the same density as water and a diameter of d μm falling through air at 20 °C is:

$$v_s = 0.00308\, d^2 \qquad (2)$$

For non-spherical spores v_s can be estimated from that of a spherical spore of the same volume, v_{ss}, by dividing by a shape factor, α ($v_s = v_{ss}/\alpha$). Shape factors have been evaluated for a number of simple shapes such as ellipsoids, cylinders and discs (Mercer, 1973; Chamberlain, 1975). McCartney *et al.* (1993) showed that v_s for *Alternaria* sp. conidia could be estimated from that of cylinders with the density of water and the same length, L, and mean diameter, d, of the spores. At 20 °C, v_s (cm s^{-1}) of such spores is approximated by:

$$v_s = \frac{0.00404\, d^2 (L/d)^{2/3}}{\alpha} \qquad (3)$$

where d is in μm and the shape factor, α, is a function of L/d. For cylinders with L/d values up to about 5, $\alpha = 0.087(L/d) + 0.97$ (Chamberlain, 1975). For cylinders with large values of L/d, v_s may depend only on d (Mercer, 1973). Using the shape factor values for glass fibres given by Mercer (1973) v_s (cm s^{-1}), at 20 °C, of long thin spores, such as *Claviceps purpurea* ascospores, with L/d between 50 and 150 can be estimated to within about 2% (assuming that they have the same density as water):

$$v_s = 0.0117 d^2 \qquad (4)$$

where d is in μm. Table 1 illustrates the relationship between fall speed and particle diameter for spheres, spheroids, cylinders and fibres.

Fungal spores may also be dispersed in clusters or chains (McCartney, 1997). The value of v_s for a cluster of spores is usually larger than that for a single spore, but less than that for a sphere of the same volume. Ferrandino and Aylor (1984) found that the settling speed of clusters of *Uromyces phaseoli*, and *Lycopodium clavatum* spores and *Ambrosia elatior* pollen could be estimated from:

$$v_{sn} = 0.98 v_s n^{0.53} \qquad (5)$$

where n was the number of spores in the cluster and v_s was the settling speed of a single spore. Equation 5 also described the relationship between v_s for of a single *Blumeria graminis* conidium and clusters of conidia (McCartney

and Bainbridge, 1987). But, v_{sn} for chains of *Alternaria* sp. conidia were better described by Equation 3 with L the length of the chain and d the mean diameter (McCartney *et al*., 1993).

The settling speed of a spore clearly influences its potential for dispersal. However, a spore's aerodynamic properties also affect deposition processes such as rate of sedimentation and efficiency of impaction (see below). The aerodynamic characteristics of a spore can be summarised using the concept of an "aerodynamic diameter," d_a. This is the diameter of a sphere with the density of water that has the same aerodynamic behaviour as the spore. The aerodynamic diameter of a spore can be calculated from Equation 1 by setting ρ = 1 g cm^{-3} and solving for d. In air at 20 °C, d_a (in μm) for a spore of settling speed v_s is:

$$d_a = 18.02\sqrt{v_s} \qquad (6)$$

when v_s is measured in cm s^{-1}.

SPORE RELEASE

As in any forms of air transport, fungal spore dispersal has three distinct phases: take-off, flight and landing. Thus, before spores can be dispersed they need to become airborne, and because spores are very small, this entails escaping the boundary layer of nearly still air on the surface on which they are growing (Figure 1). Spores can be passively released into the air by for example gusts of wind, mechanical disturbance (e.g., animal movement or rain tapping a leaf) or by rain splash, but many fungi have developed mechanisms that actively release their spores into the air (Ingold, 1971). These mechanisms are complex and varied and have been discussed at length by several authors (Ingold, 1971, Lacey, 1986, Lacey, 1996, Ingold, 1999). Most of the fungi that employ an active spore release mechanism are basidiomycetes and ascomycetes (Ingold, 1999) although fungi in other genera also actively liberate spores. Ballistospore discharge in basidiomycetes rarely projects spores further than a few mm (Ingold, 1999), whereas ascospore discharge in ascomycetes usually propel spores 0.5–2 cm, but distances up to 40 cm have been reported for some species (Lacey, 1996). Many active release mechanisms require water, for example the "squirt-gun" mechanism common in many ascomycetes, but in some fungi or Oomycetes, spore liberation takes place under dry conditions (Lacey, 1996). For example, sporangiophores of *Phytophthora infestans* and *Peronospora tabacina* twist in response to changes in relative humidity with sufficient violence to release sporangia.

Active spore release is often driven by environmental factors such as temperature, humidity and light, but is often related to water requirements. Ascospores are usually released after wetting by rain or dew, as water is needed for the release mechanism (Lacey, 1986, 1996). For example, periods of *Pyrenopeziza brassicae* ascospore release in oilseed rape crops are associated with rain, but spore release can continue for up to five days without further rainfall as the crop debris, on which the fruiting bodies develop, continues to respond to wetting and drying cycles caused by dew (McCartney and Lacey, 1990). Similarly, ascospores of *Leptosphaeria maculans* (phoma stem canker of oilseed rape) are released after rain, and can exhibit a diurnal periodicity with most spores being released between 10:00 and 12:00, possibly due to changes in relative humidity (West *et al*., 2002). Other fungal groups that use active spore release, such as some *Entomophthorales*, also exhibit diurnal periodicities in spore concentrations. Conidia of *Erynia neoaphidis*, a pathogen of aphids, tend to be released during the night or in the early morning (01:00–07:00) when environmental conditions favour spore production (Hemmati *et al*., 2001).

In contrast to fungi that have developed active spore release mechanisms, many fungi rely on external physical forces to release their spores into the air. Wind can release spores directly by blowing them off surfaces or by dislodging them by shaking the surface on which the fungus is growing (Bainbridge and Legg, 1976). Many fungi have evolved spore bearing structures that hold the spores away from the surface to enhance their chances of being blown off. Powdery mildews, such as *Blumeria graminis,* produce conidia in chains, the oldest

spores being raised away from the leaf by progressively produced spores. Spores are removed by wind when the aerodynamic forces acting on the spore exceed the attachment forces (Aylor and Parlange, 1975), but these forces are not known for most fungi. The wind speeds needed to remove spores are probably relatively large (Grace, 1977), for example, conidia of *Blumeria graminis* are only released in wind speeds exceeding about 0.5 m s^{-1} (Hammett and Manners, 1974), while wind speeds exceeding 5 m s^{-1} are needed to remove conidia of *Drechslera maydi* (southern leaf spot of maize) (Aylor, 1975). It is therefore likely that in many environments spore release by wind takes place only in gusts when speeds are sufficient to remove spores. Thus wind intermittency (turbulence) probably plays an important role in spore removal (Aylor, 1978; Aylor *et al.*, 1981). The importance of gusts in the removing spores has been demonstrated in wind tunnel experiments using conidia of *Passalora personata* (late leaf spot of groundnut) (Wadia *et al.*, 1998).

Spores can also be released into the air by other mechanical actions such as crop disturbance by machinery: combined harvesters release large numbers of spores into the air. Mechanical disturbance can also be responsible for spore release in industrial and indoor environments, for example waste composting and processing cork oak (Avila and Lacey, 1974; Lacey *et al.*, 1992; Lacey, 1997). Spores released in such environments can represent potential health risks to workers. Cleaning operations in food factories have been shown to generate aerosols containing microorganisms (Burfoot *et al.*, 2003) and such activities could easily remove and disperse fungal contaminants growing on surfaces. Rain drops falling on leaves or other surfaces dislodge "dry" spores to allow them to be dispersed by wind. Some plant pathogen spores can be released into the air in this manner, for example late leaf spot of groundnut (*Passalora personata*) (Wadia *et al.*, 1998) and brown (*Puccinia recondita*) and yellow (*P. striiformis*) rust of wheat (Geagea *et al.*, 2000). Spores of some puff-balls (*Lycoperdaceae*) and earth stars (*Geastraceae*) can be ejected into the air when raindrops strike their ripe fruiting bodies.

Rain or spray can remove spores directly from surfaces in run-off water or in splash droplets (Madden, 1992). Raindrops striking surfaces can remove spores by incorporating them in the droplets produced by splash. The spores of many plant pathogens can only be dispersed by water (usually splash) because they are contained in mucilage which prevents dispersal by wind (Fitt *et al.*, 1989). The droplets produced by rain splash range in size from a few μm to up to 1-2 mm, but spores tend to be carried in droplets greater than about 50 μm and most spore-carrying droplets tend to be between about 300 and 700 μm (Fitt *et al.*, 1989). As the fall speed of most spore carrying droplets is relatively large (between 1 and 3 m s^{-1}) they tend to be quickly deposited and are therefore not efficiently dispersed by wind. However, the smaller droplets can evaporate leaving the spores effectively airborne.

DISPERSAL

Once spores have become airborne they can be transported by wind. If air flow were steady and non-turbulent, then the distance, x, a spore would travel could be calculated simply from its fall speed, v_s, the wind speed, u and the height, h, from which it was released:

$$x = \frac{h.u}{v_s} \qquad (7)$$

Unfortunately, natural winds (and many indoor air flows) are turbulent, which causes the concentration of spores in a spore plume to be diluted as the plume expands downwind, in a manner analogous to a smoke plume. Because of this it difficult to define the "dispersal distance" for windborne spores. Spore dispersal is therefore often described in terms of a spore concentration or dispersal gradient that describes how concentration changes away from the spore source (Gregory, 1973). Patterns of spore concentration gradients round spore sources are complex, but, spore concentrations measured in one direction away from the source decrease monotonically with distance

(Figure 3). Several different functions have been used to describe dispersal gradients (Minogue, 1986; Fitt *et al.*, 1987; McCartney and Fitt, 1998).

Two simple functions have been extensively used to describe dispersal gradients: the negative exponential function:

$$C = C_0 \exp(-\alpha x) \quad (8)$$

and the inverse power function:

$$C = Ax^{-\beta} \quad (9)$$

Where C is spore concentration, x is the distance from the source and C_0, α, A and β are constants. The coefficients α and β determine the rate of decrease in spore concentration with distance, and are sometimes referred to as "dispersal gradients". Although both functions appear to behave in a similar manner, they are fundamentally different (Figure 3). In the negative exponential, concentration decreases by half over fixed distances (half distance, $d_{½} = 0.693\alpha$, analogous to "half life" in radioactive decay). The idea of a "half distance" is frequently used to describe spore dispersal gradients (Table 2). In the inverse power law, the rate of decrease in concentration decreases with distance from the source giving a "long tailed" distribution.

The negative exponential equation is more appropriate when concentration depletion is predominantly by deposition (as in crop canopies), but the inverse power equation is more suited when turbulent mixing is dominant (McCartney and Fitt, 1998). Thus, a power law is usually more appropriate when describing dispersal over long distances (Brown and Hovmøller, 2002).

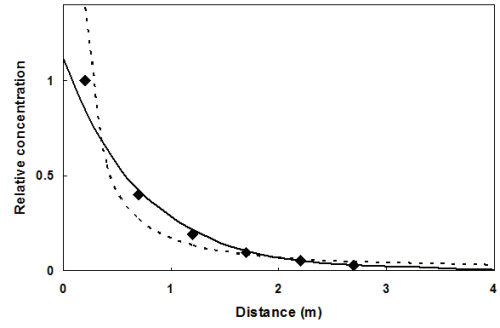

Figure 3. Spore dispersal gradients. Concentrations of airborne *Puccinia striiformis* (yellow rust) conidia measured downwind of an infected patch in a wheat field (◆). Solid line: negative exponential function fitted to the measured concentrations; broken line: inverse power function fitted to the measured concentrations (West and McCartney, unpublished data).

Table 1. Relationship between fall speed (v_s) and particle diameter for spheres, spheroids, cylinders and fibres. The density of the particle was assumed to be that of water. Fall speeds are given in cm s^{-1} when diameters are in μm. Shape factors were taken from Chamberlain (1975) and Mercer (1973). The shape factors for glass fibres estimated from Mercer (1973) were used to calculate the relationships for fibres. The ration of fall speed/ fall speed of a sphere of the same volume (v_s / v_{ss}) is given in the third column, and the aerodynamic diameter, d_a, in the fourth column. These relationships only hold for particles with d_a between about 1 and 60 μm.

Shape	v_s (cm s^{-1})	v_s / v_{ss}	d_a
Sphere	0.00308 d^2	1	D
Spheroid (height/diameter = 0.75)	0.00251 d^2	0.99	0.90 d
Spheroid (height/diameter = 0.5)	0.00186 d^2	0.96	0.78 d
Spheroid (height/diameter = 0.2)	0.00085 d^2	0.80	0.53 d
Spheroid (height/diameter = 0.1)	0.00045 d^2	0.67	0.38 d
Cylinder (length/diameter = 1)	0.00382 d^2	0.95	1.11 d
Cylinder (length/diameter = 2)	0.00561 d^2	0.87	1.35 d
Cylinder (length/diameter = 5)	0.00841 d^2	0.71	1.65 d
Fibre (length/diameter = 50)	0.0115 d^2	0.21	1.93 d
Fibre (length/diameter = 100)	0.0118 d^2	0.14	1.95 d
Fibre (length/diameter = 150)	0.0119 d^2	0.10	1.96 d

Table 2: Spore concentration or deposition gradients: values are given as half distances[1]. The entries are ordered in approximately increasing aerodynamic diameter.

Species[2]	Half distance[1] (m)	Spore shape[3] and size (μm)	Comments	Source
Pyrenopeziza brassicae	7-10	rounded cylinder ~12 x 2.4	Light leaf spot of oilseed rape, concentration downwind from field edge.	McCartney *et al.* (1986)
Scerotinia sclerotiorum	0.2–0.9	ellipsoid ~8 x 3	Ascospore deposition downwind of pasture plots inoculated with *S. sclerotiorum* sclerotia.	Bourdôt *et al.* (2001)
Bovista plumbea	5-8	ovoid 4-5.5 x 5-6.5	Grey puffball.	Fitt *et al.* (1987)
Cladosporium sp.	32-110	ellipsoid 10-20x3-4	Spores, concentration downwind from a wheat crop.	From: Eversmeyer and Kramer (1992)
Cryphonectria parasitica	43	ellipsoid 7-12 x 3-5.5	Chestnut blight.	Fitt *et al.* (1987)
Gibberella zeae	11-33	curved fusoid 19-24 x 3-4	Fusarium head blight of wheat, concentration downwind of infected wheat plots.	de Luna *et al.* (2002)
Ustilago scitaminea	1.1–4.6	spheroid 5.5-7.5	Smut of sugar cane, deposition to the ground close to infected plants.	Hoy *et al.* (1991)
Ustilago violacea	1.4	spheroid 4-10	Anther smut of white campion, deposition to flowers and ground traps.	Roche *et al.* (1995)
Venturia inaequalis	8–11	ellipsoid ~12 x 5	Apple scab, ascospores, estimated from average spore concentrations measured over a season.	From Holb *et al.* (2004)
Botrytis cinerea	1.5–2.4	ellipsoid ~13 x 7	Gray mould of snap beans, deposition to leaves during crop bloom.	From: Johnson and Powelson (1983)
Podaxis pistillaris	6-7	ovoid 9-12 x 10-14	Desert shaggy main mushroom.	Fitt *et al.* (1987)
Phaeoisariopsis personata	0.4-1	rounded cylinder 18-60 x 6-10	Late leaf spot of groundnut, deposition estimated from "trap" plants.	Savary and Van Santen (1992)
Blumeria graminis	~1.8	ellipsoid 25-40 x 8-10	Barley powdery mildew, within a barley canopy.	From: Bainbridge and Stedman (1979)
Blumeria graminis	20-89	ellipsoid 30 x10	Wheat powdery mildew, concentration downwind from a wheat crop.	From: Eversmeyer and Kramer (1992)
20 μm drops	0.25–2.5	spheroid 20	Deposition to horizontal collectors in a barley crop.	McCartney and Bainbridge (1984)
Tilletia tritici	5.5–7.5	spheroid 14-25	Bunt of wheat.	Fitt *et al.* (1987)
Puccinia recondita	0.5-1.2	ellipsoid 16-34 x 13-25	Wheat rust, deposition to "trap" wheat plants in a winter barley crop.	Aylor (1987)
Puccinia recondita	12.5-24	ellipsoid 16-34 x 13-25	Brown rust of wheat, concentration downwind from a wheat crop.	From: Eversmeyer and Kramer (1992)

Puccinia striiformis	0.5	spheroid 20-25	Yellow rust of wheat, concentration downwind of an infected patch in a wheat crop.	Figure 3
Alternaria linicola	1.6–2.3	club shape 60-220 x 15-21	Alternaria blight of linseed, concentration downwind of line source in a linseed crop.	Vloutoglou *et al.* (1995)

[1] Half distances were estimated from original data when not quoted in the source.
[2] Latin binomials are currently accepted usage, and may differ from those quoted in the original source.
[3] Sizes of spheroids are given as the diameter; for ellipsoids and other shapes, the size is given as length x diameter.

When both functions have been compared using measured spore or pollen gradients, both models often fit equally well (Gregory, 1968, Fitt *et al.*, 1987, Ferrandino, 1996). Local environment can play an important role. Within crops, gradients are generally relatively steep (Table 1), for example $d_{½}$ values for 20 μm droplets measured within a barley crop ranged between about 0.5 and 2.5 m depending on the canopy structure (McCartney and Bainbridge, 1984).

Gradients at the edges of crops tend to be shallower (Table 2): $d_{½}$ values measured for oilseed rape pollen (v_s value about 1.6 cm s^{-1} compared to about 1.2 cm s^{-1} for 20 μm drops) dispersing from the edge of an oilseed rape field were between about 2 and 8 m (McCartney and Lacey, 1991). Spore size (aerodynamic diameter) can also affect dispersal gradients: *Pyrenopeziza brassicae* ascospores, which are much smaller than oilseed rape pollen grains (v_s about 0.03 cm s^{-1}), had $d_{½}$ values of about 9 m when measured downwind from the same oilseed rape field as the oilseed rape pollen (McCartney *et al.*, 1986). Other functions have been used to describe spore dispersal gradients (McCartney and Fitt, 1998) and recently Bullock and Clarke (2000) have suggested a combined exponential and inverse power equation to describe wind-borne seed dispersal:

$$C = A(ae^{-\alpha x} + bx^{-\beta}) \qquad (10)$$

This equation allows for two different components of dispersal: a steep short distance gradient and a flatter long distance "tail". This could also be used for spores, but this equation requires two parameters to describe the shape of the gradient. Unfortunately, there has been little systematic work on the influence of environmental factors, surface structures or spore characteristics on dispersal gradient parameters. Thus it is difficult to estimate *a priori* dispersal gradient shapes.

Because of their turbulent nature, wind can also rapidly transport spores vertically into the atmosphere, where they have the potential to disperse over a large distance. Vertical transport is most likely, when turbulence is high, for example during unstable atmospheric conditions that occur during sunny afternoons (Figure 2). Such conditions also favour the passive removal of spores and escape from plant canopies. Spore concentrations decrease with height if the source of spores is local and at ground level, but concentrations can increase with height if the spores have a distant source. Spore aerodynamic diameter can also affect the potential for vertical transport of spores: concentrations of ascospores of *P. brassicae* (d_a about 3.1 μm) decreased less quickly with height than much larger oilseed rape pollen grains (d_a about 23 μm) (Figure 4). Although most fungal spores probably travel relatively short distances, once they have been mixed into the planetary boundary layer (Figure 1) they can travel long distances. Hirst *et al.* (1967) found measurable concentrations of fungal spores between 500 and 1000 m above the North Sea many kilometres from the nearest source, and spores and pollen grains, which must have been produced in distant continents, have been found in air samples taken in Antarctica (Marshall, 1996). The introduction of new plant diseases into countries has been attributed to long distance transport of spores, although such events are probably rare (Brown and Hovmøller, 2002). Natural or man-made events that enhance vertical air movement,

such as bush fires, may be responsible for individual long distance transport events, for example the spread of viable bacteria and fungal spores from the Yucatan in Mexico to Texas and from Southeast Asia to Hawaii (Mims and Mims, 2004). Long distance transport of spores need not take place in a single step: plant pathogen inoculum can spread over continental distances in multiple "jumps". In most years, tobacco blue mould (caused by *Peronospora tabacina*) spreads from Cuba up the eastern states of the USA in a series of dispersal events (Davis and Main, 1986). The North American Plant Disease Forecast Centre, North Carolina State University, Raleigh, NC, provides an Internet-based blue mould disease risk forecasting system for tobacco and cucurbit growers (http://www.ces.ncsu.edu/depts/pp/ blue mold/index.html, Main *et al.*, 2001). The forecasting system uses atmospheric dispersal models to predict *P. tabacina* spore transport events.

Empirical descriptions of spore dispersal gradients have limited applications as it is difficult to estimate gradient parameters for conditions different from those in which they were measured.

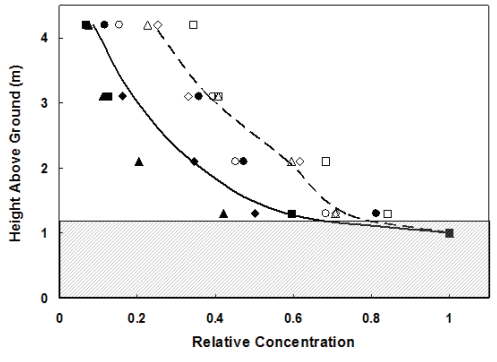

Figure 4. Vertical transport of spores. Relative concentration profiles of *Pyrenopeziza brassicae* ascospores and oilseed rape pollen measured simultaneously above an oilseed rape crop: filled symbols pollen; open symbols ascospores. The solid line is the mean profile for the pollen and the broken line is that for the ascospores (McCartney and Lacey (1991) and McCartney, unpublished data).

As a result, atmospheric dispersal models that are used to calculate air pollution dispersal have been adapted to estimate spore dispersal patterns (McCartney and Fitt, 1998). Average pollution concentrations downwind of point and line sources can be estimated using Gaussian Plume dispersal models (Pasquill and Smith, 1983). Some atmospheric dispersal models that have been developed for use in air pollution regulation and emergency planning are of this type (Caputo *et al.*, 2003). For example, the US Environmental Protection Agency developed the AEROMOD model for regulatory purposes (USEPA, 1999). Gaussian Plume models assume that air pollutant concentration profile distributions are Gaussian in both crosswind and vertical directions (Figure 5). The values of the standard deviations of the crosswind (σ_y) and vertical (σ_z) distributions are dependant on downwind distance and determine the downwind gradients. As Gaussian plume models have been used for many years, much effort has been spent on parameterising σ_y and σ_z for different atmospheric conditions (Pasquill and Smith, 1983). Gaussian Plume models were developed in the 1980s to assess the risk of the aerial transmission of Foot and Mouth disease in farm animals (Blackall and Gloster, 1981; Gloster, 1983a) and Newcastle Disease in poultry (Gloster, 1983b). This type of model was also used in the management of the 2001 Foot and Mouth outbreak in the UK (Mikkelsen, 2003).

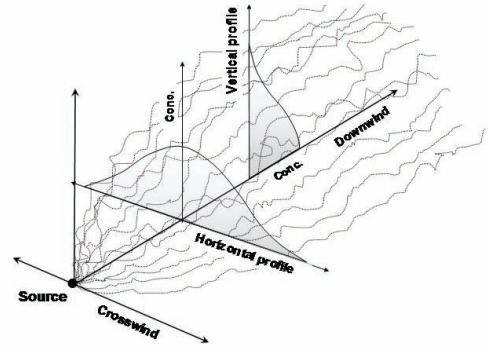

Figure 5. Spore dispersal downwind of a ground level point source. Gaussian plume models assume that the spore concentrations in the crosswind and vertical directions are distributed according to a Gaussian distribution.

Air parcel trajectory analysis has been used in tracing potential long distance spread of plant pathogens (Aylor, 1986, Davis, 1987, Brown and Hovmøller, 2002). Trajectory analysis uses information on wind fields and atmospheric temperature profiles to account for large scale movement of air parcels due to changes in wind direction, and is frequently used in air pollution analysis (Stohl, 1998). Web-based trajectory models are available from the USA National Ocean and Atmosphere Administration (HYSPLIT model http://www.arl.noaa. gov) and the British Atmospheric Data Centre (NERC Centres for Atmospheric Science, http://badc.nerc.ac.uk/ community/). Trajectory analysis can be combined with the Gaussian Plume approach to take account of spore dispersal within the air parcel (Aylor, 1986; Davis, 1987; Aylor, 1999). The spore plume is treated as an expanding "puff" travelling along the path of the trajectory. The spore concentrations in the "puff" are assumed to follow a Gaussian distribution in the vertical, horizontal and downwind directions, unless constrained by atmospheric structures such as inversions. The rate of "puff" expansion is determined by how σ_z, σ_y and σ_x (the standard deviations of the Gaussian distributions) change with distance. Gaussian "puff" models for spore dispersal also allow for spore loss through deposition by sedimentation and washout (Aylor, 1999). The model used by the North American Plant Disease Forecasting Centre for their Internet-based tobacco and cucurbit disease risk forecasting system is a Gaussian "puff" trajectory model (Main *et al.*, 2001). The NOAA HYSPLIT model is used to estimate the risk of inoculum movement from infected to uninfected areas. A Gaussian "puff" model was also one of the dispersal models used to analyse the Foot and Mouth disease outbreak in the UK in 2001 (Mikkelsen *et al.*, 2003).

Other models, based on physical principles, have been used to describe airborne spore dispersal (see for example: Aylor, 1990; McCartney, 1997; McCartney and Fitt, 1998; Aylor *et al.*, 2003).

EAD models spore dispersal is assumed to be analogous to molecular diffusion; while LS models estimate the trajectories of "individual spores" allowing for the effects of turbulence.

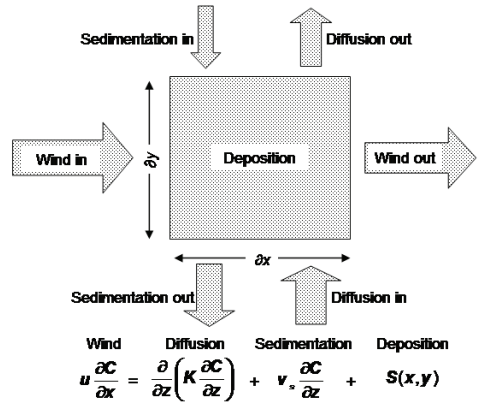

Figure 6. Eulerian advection-diffusion models are based on the number balance of spores entering and leaving a small volume of air. Schematic diagram for an infinite line source of spores (assumes that cross-wind diffusion ignored and downwind diffusion negligible compared to downwind transport). The difference between the rate the spores carried into and out of the volume by wind is balanced by the rate at which spores enter and leave the volume vertically (sedimentation and diffusion) and the rate at which spores are deposited within the volume (deposition). The rate of diffusion is proportional to the vertical concentration gradient (∂C/∂z).

EAD models are based on the number balance of spores entering and leaving a small volume of air (Figure 6). This can be illustrated by considering an infinite line source of spores at right angles to the wind. In this case, cross-wind and downwind diffusion can be ignored (advection is assumed to be the predominant mechanism for transporting spores downwind). For a small volume of air, the difference between the rate at which spores enter or leave the volume horizontally by wind is balanced by the rates at which spores leave the volume vertically by diffusion or by sedimentation and the rate at which spores are removed from the volume by deposition (Figure 6). The rate of vertical diffusion is assumed to be proportional to the vertical concentration gradient ($K_z\partial C/\partial z$) and determined by a diffusion coefficient, K_z, which is a function of height. Dispersal from point and area sources can also be described by EAD models, but these require terms to describe horizontal diffusion and advection (Yao *et al.*, 1997, Aylor, 1999). EAD models usually need to be solved by numerical methods, and

diffusion coefficients, wind speeds and spore deposition rates need to be defined for all points in the model space. Diffusion coefficients and wind speeds can be measured directly or estimated theoretically for different atmospheric conditions (Yao *et al.*, 1997; D'Amours, 1998). Deposition rates depend on spore aerodynamic properties and the nature of the surface (see next section). EAD models implicitly assume that the size of the eddies that cause diffusion are small compared with the size of the dispersing plume. This may not be the case in some situations, such as in plant canopies, which may explain why EAD models have been found to overestimate concentrations of plant pathogen spores close to the spore source (Legg and Powell, 1979; Aylor and Ferrandino, 1989). However, EAD models are useful when the dominant eddies are small compared with the vertical width of the plume (Aylor, 1999), such as dispersal downwind from the edge of a field (Yao *et al.*, 1997). Xu and Burfoot (2000) have applied EDA-based models to the application, by fogging, of agrochemicals to potatoes in storage.

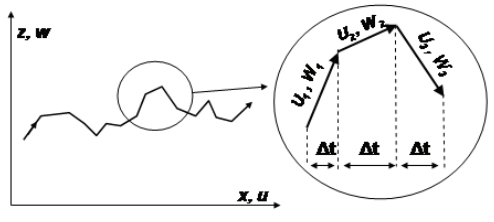

Figure 7. Schematic diagram of a two-dimensional Lagrangian stochastic dispersal model. The horizontal (u) and vertical (w) wind speeds are recalculated after each time step (Δt). The speeds are calculated from the previous speed plus a random component to simulate turbulence.

Lagrangian stochastic, LS, models simulate the paths of individual spores as a pseudo-random walk (Figure 7). Spore paths are simulated as series of discrete steps determined partly by a correlation between successive velocities (the velocity "memory") and partly by a random element that represents the effects of turbulence (Figure 7). The formulation of LS models has been reviewed by Wilson and Sawford (1996). Because LS models simulate the flights of "individual spores", they are useful for estimating dispersal close to sources (Aylor, 1989, 1999) and have been used to calculate the escape of *Venturia inaequalis* (apple scab) ascospores from the ground (Aylor and Flesch, 2001) and *Phytopthora infestans* (late blight) sporangia from potato canopies. The dispersal of pollen from maize crops has also been investigated using LS models (Aylor *et al.*, 2003; Jaroz *et al.*, 2004). The effects of gust release on spore dispersal can be simulated using LS models, by only starting spore trajectory simulations when the wind speed exceeds the spore release threshold. LS simulations suggest that deposition near the source may be enhanced by gust release due to more efficient impaction at the higher wind speeds in which the spores are travelling (see below) (Legg, 1983). LS models have the potential to describe spore dispersal in a wide range of environments as long as the flow fields can adequately be described (mean flow and turbulence statistics). Mean flow fields in indoor environments can be calculated using sophisticated computational fluid dynamics (CFD) programs that solve the continuity equations for mass and momentum (Burfoot *et al.*, 1999). For example such programs have been used to study the air flow in potato storage facilities (Xu *et al.*, 2002). The mean flows predicted by CFD programs can be combined with appropriate descriptions of turbulent fluctuations to form the basis for LS particle dispersal models (Burfoot *et al.*, 1999, Riddle *et al.*, 2004). This approach has recently been used to model the dispersal of airborne microbial particles from cleaning operations in an enclosed room (Harral and Burfoot, 2005). In this study dispersal of aerosol particles generated by a boot scrubber, in a room ventilated by ceiling air ducts, was simulated using two different CDF/ Lagrangian modelling approaches (Gosman and Ioannides, 1981; Reynolds, 1998). Both modelling approaches predicted the general pattern of particle dispersal within the room, but the Reynolds model more accurately predicted particle clearance times. The Reynolds model simulates the effects of velocity fluctuations more accurately than the Gosman and Ioannides model, and therefore may be more applicable to modelling the dispersal of microorganisms indoors. As our un-

derstanding of indoor and outdoor air flow increases, the accuracy and applicability of LS models should increase.

Atmospheric dispersal models are becoming increasingly more sophisticated, for example some can describe dispersal over complex terrain (e.g., Aloyan, 2004; Wang and Ostoja-Starzewski, 2004). These new approaches could help in understanding the influence of landscape on spore dispersal. As noted above, the combination of computational fluid dynamic models with dispersal models should allow spore dispersal to be modelled in urban (Riddle *et al*., 2004) and indoor environments (Harral and Burfoot, 2005).

DEPOSITION

The rate of deposition of spores, (*D*, number per unit area per unit time) from the atmosphere to a horizontal surface is proportional to the concentration of spores above the surface, *C*, and is given by:

$$D = v_d C \qquad (11)$$

the constant of proportionality, v_d, is called the deposition velocity (Chamberlain, 1975). If atmospheric air flow was non-turbulent, v_d would have the same value as the spore settling speed, v_s. However, in turbulent flow diffusion can enhance deposition rates and so deposition velocities tend to be about 2-5 times larger than v_s (McCartney and Fitt, 1985). Deposition velocities also tend to increase with wind speed and turbulence (Davidson *et al*., 1982; Callander and Unsworth, 1983). However, the effects of turbulence on spore deposition tend to decrease with increasing aerodynamic diameter (Figure 8). There have been several models developed to estimate particle deposition velocities from surface characteristics, most using an EAD approach (see McCartney and Fitt, 1985; Ferrandino and Aylor, 1985) and more recently using LS models (Reynolds, 2000).

Spores not only settle on surfaces, they can also be impacted onto an object, such as a leaf, or to the effects of inertia (Figure 9).

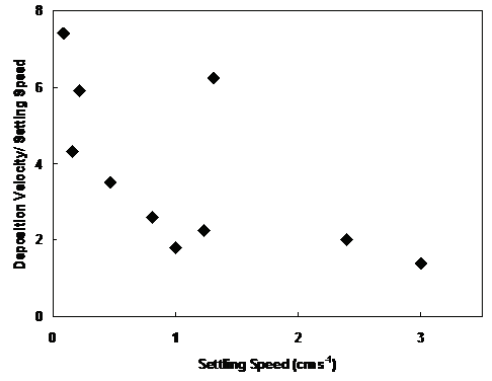

Figure 8. Enhancement of deposition by turbulent diffusion. The ratio of deposition velocity/ settling speed (v_d/v_s) plotted against settling speed for spore and pollen deposition to microscope slides 20 cm above a barley crop. The ratio decreases with increasing spore size showing that turbulence has a smaller effect on large spores. Adapted from McCartney *et al.* (1985).

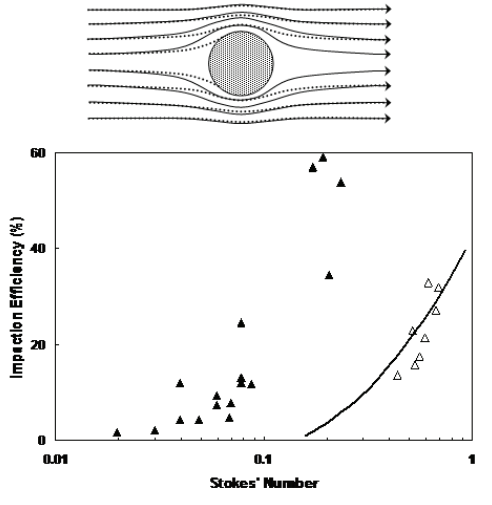

Figure 9. Top: Inertial impaction of spores. Air flow around a vertical cylinder: air streamlines are shown as solid lines (—); spore trajectories (·····) cannot follow the streamlines exactly, so some spores may strike the cylinder. Bottom: Impaction efficiencies measured in a barley crop for *Blumeria graminis* conidia as a function of Stokes' number (see text). Solid symbols (▲): measurements made inside the crop; open symbols (△): measurements made at the top of the crop. The solid line is the relationship between efficiency and Stokes' number for low turbulence flow (Chamberlain, 1975). Adapted from McCartney (1991).

The rate of dep sition by impaction, I, is proportional to the wind speed, u and the spore concentration, C:

$$I = CuE \qquad (12)$$

the constant of proportionality, E, is called the efficiency of impaction, and increases with spore aerodynamic diameter and wind speed, but decreases as the size of the object impacted upon increases (Chamberlain, 1975). In laminar flow the efficiency of impaction is a non-linear function of the particle Stokes' number, St, defined as:

$$St = \frac{v_s u}{gL} \qquad (13)$$

where g is gravitational acceleration (9.81 m^2s^{-1}) L is a characteristic length of the object (e.g., width of a leaf or diameter of a stem). Aylor (1982) gives the following functional representation for the relationship between E and St:

$$E = \frac{0.86}{1 + 0.442 St^{-1.967}} \qquad (14)$$

McCartney and Bainbridge (1987) found that impaction efficiencies for *Blumeria graminis* (barley powdery mildew) conidia measured in a barley crop were significantly larger than those calculated from Equation 14 using measured mean wind speeds (Figure 9). They attributed this to the effects of releasing spores only in gusts. Spores released in gusts will be carried in air travelling faster than the mean wind, consequently their impaction efficiencies will be larger than that for spores travelling at the mean wind speed (Aylor *et al.*, 1981). Model calculations suggest that enhanced impaction due to gusts could decrease dispersal distance close to the source (McCartney, 1987).

Deposition to individual surfaces, such as leaf elements within vegetation canopies, has often been treated as a combination of two processes: gravitational settling and inertial impaction (McCartney and Fitt, 1985). Non-horizontal and non-vertical objects are resolved into areas projected horizontally (along the mean wind direction) and vertically to determine the proportions of the total deposition that are by sedimentation (horizontal) and impaction (vertical). Thus, for an object at an angle, θ, to the horizontal the deposition rate is given by:

$$D_\theta = D_0 \cos(\theta) + D_{90} \sin(\theta) \qquad (15)$$

where D_0 and D_{90} are the deposition rates on equivalent horizontal and vertical surfaces. This assumption may not strictly be valid as the variable boundary layer on the sloping surface has a vertical component that may affect sedimentation. However, Equation 15 was found to describe deposition on sloping surfaces in a wheat canopy (McCartney and Aylor, 1987) and thus may be adequate for practical purposes.

CONCLUSIONS

Airborne transfer of microorganisms is now seen as significant route for contamination in many sectors of the food industry (Burfoot *et al.*, 2000). Thus, an understanding of the physical and biological processes involved in the aerial transport of such organisms is needed to assess the risks of contamination and to develop appropriate strategies to avoid contamination. In this chapter we have attempted to highlight the physical and biological nature of the dispersal of fungal spores through the air. Although many of the examples cited have been related to the spread of plant pathogenic fungi, the mechanisms involved are equally applicable to dispersal in other environments.

Recent advances in fluid dynamics (Reynolds, 1998) combined with new methods for detecting and identifying fungal contaminants (Ward *et al.*, 2004) offer new opportunities for in-depth studies of the spread of contaminants in indoor and outdoor environments. Such studies, in turn, will lead to a better understanding of the role dispersal plays in fungal contamination and allow improvements to be made in both the risk assessment and the management of contamination.

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